

SEASONAL PHENOLOGY AND POSSIBLE MIGRATION OF THE
MOURNING CLOAK BUTTERFLY *NYMPHALIS ANTIOPA*
(LEPIDOPTERA: NYMPHALIDAE) IN CALIFORNIA

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ABSTRACT. — Circumstantial evidence is presented that suggests the Mourning Cloak undergoes regular seasonal up- and downslope movements in northern California. The species breeds at low elevations in spring and then disappears until autumn; its disappearance coincides with the appearance of fresh individuals in the Sierra Nevada alongside obvious hibernators.

The Mourning Cloak or Camberwell Beauty, *Nymphalis antiopa* L., is one of the most characteristic Holarctic butterflies; it ranges from the subarctic to the subtropics. Nonetheless, its basic biology is poorly known. There have been many discussions of its rare and intermittent occurrence in the British Isles (Williams et al. 1942, Williams 1958, Chalmers-Hunt 1977), but only one detailed description of its natural history—that by Young (1980), who narrated the situation in Wisconsin, USA, in the hope that it would help Palearctic workers understand the dynamics of their own populations. The biology of *N. antiopa* in California, USA, is quite different; specifically, it seems to involve either estivation or altitudinal migration or both. Altitudinal migration appears to occur in California populations of *N. (Aglaia) milberti* Latr. and *N. californica* Bdv. (Shapiro 1973, 1974a, 1974b, 1975, 1979, 1980).

Since 1972 phenological data have been taken for all butterflies at a series of stations forming a transect parallel to Interstate Highway 80 from sea level at the Suisun Marsh, Solano County, to tree-line at Castle Peak, Nevada County (2750m). Each station is visited at roughly two-week intervals throughout the butterfly season, and all species flying are recorded. Figures 1 and 2 represent the *N. antiopa* data from this transect for 1983 and 1984. These two years were extremely different meteorologically and essentially embrace the range of variation observed during the 13 years of the study. The year 1983 was one of

record high precipitation, with both rainfall and snowpack greater than 200% of the 30-year means. Summer was cool and unusually moist, after a very late and cloudy spring. Precipitation in the 1983-84 season was slightly below normal. Rain- and snowfall were heavy before Christmas and nearly nonexistent thereafter. Spring was early and hot, and summer 1984 was the hottest of record (over 125 years) at low elevations and much warmer than normal in the mountains, with an unusual frequency of thunderstorms. The fact that the seasonal patterns of *N. antiopa* are consistent in two such different years suggests that they accurately represent the seasonal dynamics of the animal.

Shapiro (1974c) reported that *N. antiopa* was univoltine in the Sacramento Valley despite the very long growing season. Nearer the coast, at the Suisun Marsh, Shapiro (1974d) reported essentially the same phenology. The same pattern was again reported for suburban Sacramento by Smith (1983). Smith provides counts of sightings at one specific locality for the years 1970 through 1982. His pattern is quite consistent, with no animals seen after 8 July in 50% or more of years, after a very dramatic peak between 20 May and 1 July. It was initially assumed by Shapiro that the single spring brood in these areas entered estivation, followed by a brief period of activity in autumn, followed by hibernation, such that Sacramento Valley animals lived a full year as adults. Although estivation remains a possibility, no estivating adult has been found

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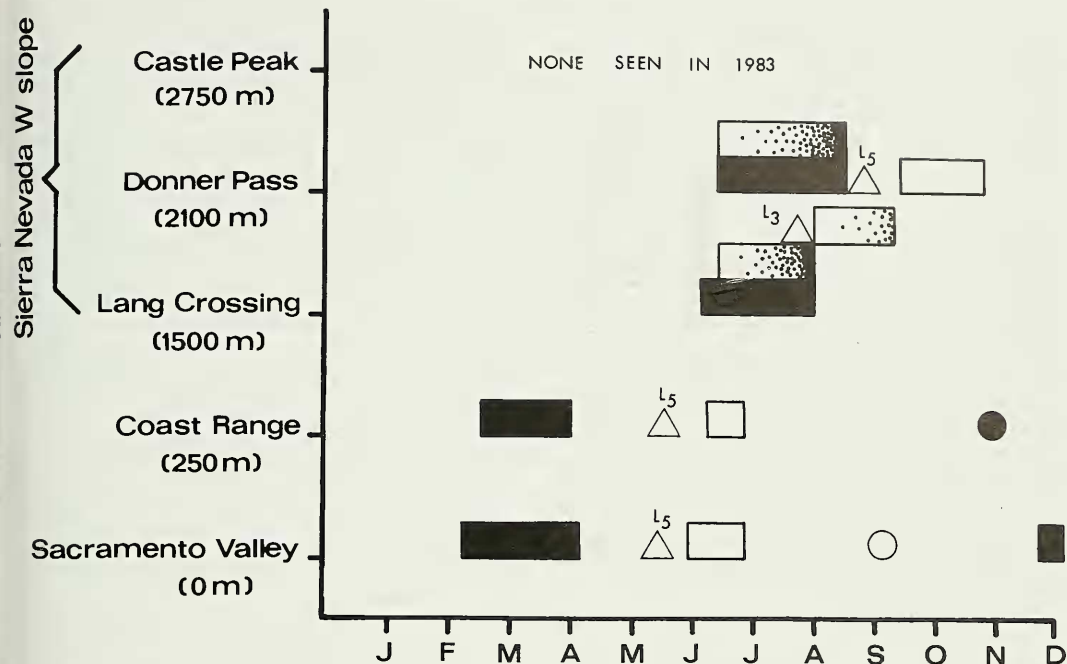


Fig. 1. Phenology of *Nymphalis antiopa* along a transect across northern California in 1983. Intensity of stippling indicates degree of wing wear. Dots are individual occurrences. Triangles are observations of larval colonies: L₃=third instar, etc.

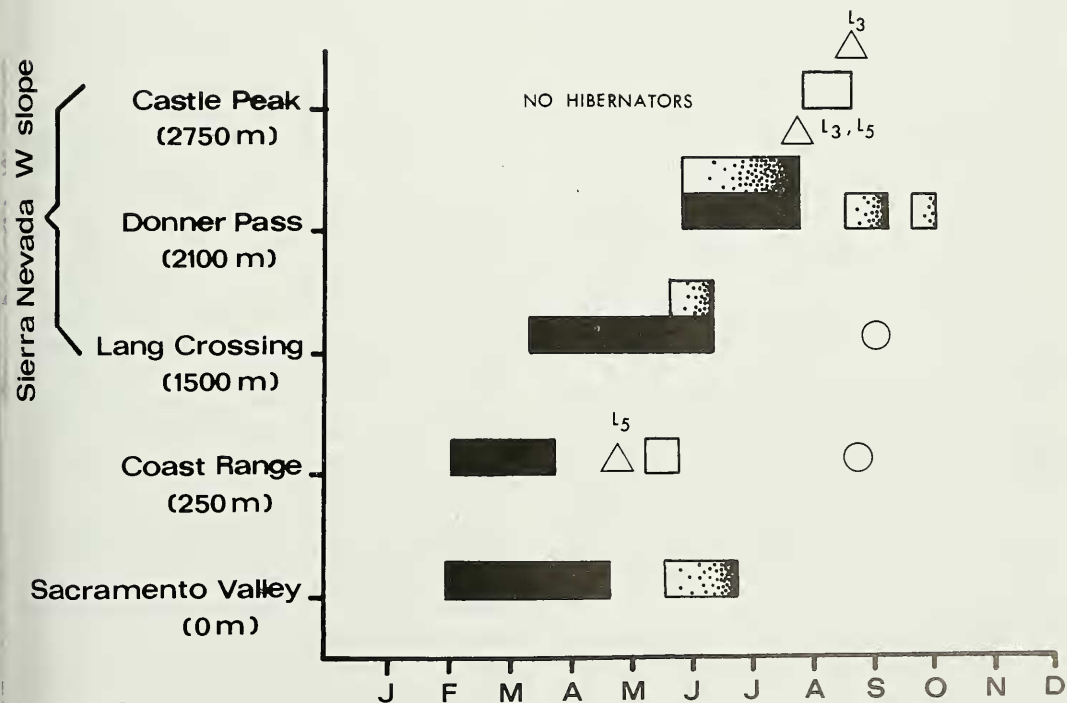


Fig. 2. Same for 1984.

in 13 years, the condition of the adults observed in autumn and early winter argues against it, and, most importantly, there is a persuasive circumstantial case implicit in Figures 1 and 2 for altitudinal migration on a regular seasonal basis.

Overwintered adults in typical posthibernation condition (borders nearly or totally white, much wing wear) were observed near Sacramento and in the Inner Coast Range beginning in late winter in both years. Similar hibernators appear at montane sites shortly after snowmelt—the timing of which varied by several weeks between the two years. The single flight of fresh animals was observed at low elevations in late May–early July, lasting from 10 to 41 days in different locations. Smith (personal communication) saw singletons in Sacramento during the second, third, and fourth (three records) weeks of July and the second week of August, 1983, and on 9 July and 25 July 1984.

As can be seen from Figures 1 and 2, at mountain stations more or less fresh animals can also be found in spring, flying with the hibernators. At Lang Crossing (1500 m), for example, the first 1984 hibernators appeared on 10 March and fresh animals followed on 6 May while hibernators were still numerous. At Donner Pass (2100 m), both fresh and worn animals were already flying 27 May and continued to be distinguishable through 20 June. Thereafter, worn animals probably derived from both groups flew until 20 July. On that date two colonies each of 3rd- and 5th-instar larvae were censused, presumably representing a differential in the timing of reproduction by the two groups of adults. On 15 August fresh adults were very numerous in the vicinity of the previous L_5 colonies. By 6 September only a few were present and these were moderately worn, but a second group of fresh animals appeared 19 September and flew for a week.

At the highest station, Castle Peak (2750 m), there is no permanent population, and the species is present in some years (generally those with early snowmelt) and absent in others (generally late years). It was absent in 1983. In 1984 no hibernators were seen, but fresh animals flew 27 July–17 August, and on the latter date one colony of L_3 was found.

Given that reproduction by *N. antiopa* was late at low elevations in 1983 and that the timing of snowmelt was even more distorted, it is striking that in both years figured (and in

general) the appearance of fresh animals at mountain stations commences about a week after the valley brood appears.

Similarly, the widely scattered autumn sightings are properly timed to represent downslope dispersal by the midsummer brood reared in the mountains. Several apparently fresh *antiopa* were seen at Lang Crossing 30 August (two weeks after the flight started at Donner; no larval colonies were seen at Lang in 1984). One apparently fresh specimen was seen in Gates Canyon in the Inner Coast Range on 26 August, and Smith saw one in Sacramento on 4 September.

Nothing in these data either requires altitudinal migration or precludes estivation, but they are clearly suggestive. How plausible is the hypothesis of altitudinal migration? One alternative explanation is that *antiopa* may over-winter in both the adult and pupal stages in the Sierra Nevada. Klots (1951) raised this possibility for the eastern United States. Shapiro (1969) recorded a single case in central New York in which overwintering of the pupa seems inescapable; the animal, when captured, voided meconium. I have tried repeatedly to maintain laboratory-reared lowland California pupae at 2–3 C for extended periods, but with no success after eight weeks. True pupal diapause appears to be unknown in the Nymphalini.

Another alternative explanation for the low-altitude phenomena is a low level of reproduction in summer. In 13 years of extensive field work in the Sacramento Valley and Inner Coast Range, I have never found a single larval colony after 1 June, nor has Smith in 14 years at Sacramento. On the other hand, second broods occur occasionally beginning at Fairfield, Solano County, nearer the coast, and even a third brood has been recorded (L_5 , 20 October 1980). This is apparently standard on the immediate coast, for Tilden (1965) reports “two to three broods a year” in the San Francisco Bay area, and Emmel and Emmel (1973) report “multiple-brooded at lower elevations and single- or double-brooded in higher zones” in southern California—the “lower elevations” referring almost entirely to urban and suburban areas, not to the interior deserts. *Nymphalis antiopa* is a common urban species in Mexico City, where it breeds all year.

Some light can be shed on the annual cycle by examining the reproductive status of the animals. Although Young (1980) claims that spring populations consist solely of females—the males presumably having died overwinter—this is not true in California (or southeastern Pennsylvania or New York). In the Sacramento Valley and Coast Range, courtships and matings are observed both in autumn (occasionally) and spring (frequently). At Donner Pass they have been observed in September but not in spring. In 1984 I dissected eight August and three September Donner females. All had large amounts of fat and no well-developed oocytes, but all the August and none of the September females were virgins. All the fresh-looking females collected in the mountains in June and July have been fully reproductive ($N=15$).

Herman and Bennett (1975) reported that summer females (source population and rearing regime unspecified) eclose with large fat bodies and no oocytes, and subsequently mature as a function of environment. Maturation was essentially completed within 10 days at 25 C on LD 16:8 but did not occur after 14 days at 10 C, LD 8:16. This experiment does not separate the effects of photoperiod and temperature. Photoperiods at Donner Pass in late August are ca LD 13.5:10.5, mean temperature 16 C. Donner Pass *antiopa* reared on LD 14:10 at 25 C failed to mature after 15 weeks in the dark at 2 C.

For adult *antiopa* emerging in the Sacramento Valley in late May, photoperiods are ca LD 15:9 and mean temperature 18.9 C, conditions that should permit rapid gonadal maturation, but no reproduction is seen. Of three late May–early June Sacramento females, two had mated and one of these showed early oocytes. If altitudinal migration is real, ovarian maturation may occur during the up-slope flight, its termination coinciding with the beginning of oviposition. The distances involved (125–150 km from our Sacramento Valley sites to Donner Pass) could be traversed in a week or so, based on the progress of *N. californica* migrations I have tracked.

Shannon (1917) believed eastern U.S. populations of *N. antiopa* were at least somewhat migratory. Gibo (1981) records the species riding thermals in east central Canada; such passive soaring is associated in many insects with the initiation of long-range dispersal.

One additional aspect of the problem deserves mention. Shapiro (1981a,b) studied the canalization of the wing pattern as a trait adaptive to climate. He found that Alaskan animals are more strongly buffered physiologically against cold shock than either lowland or Sierran montane *N. antiopa*. The similarity of the physiological responses of the Californian broods, from radically different climates, could imply gene flow over the fairly short distances separating them—an interpretation consistent with the notion of altitudinal migration. Since the 1981 papers were published, the California experiments have been replicated three times with the same results for the major aberration “hygiaea.” The minor pattern differences reported in Shapiro (1981b) have been inconsistent among broods. Granted that at least part of the population of *N. antiopa* overwinters at 2100 m each year, gene flow between these and animals dispersing from the lowlands could be very substantial in some years. Such gene flow—depending on the timing of spring at both elevations—would be expected to inhibit if not prevent genetic differentiation along our altitudinal transect.

Numbers of this species are consistently too low for mark-recapture experiments to hold much promise as a test of the altitudinal-migration hypothesis. If genetic markers can be found to facilitate identification of low-elevation animals, they would be useful for documenting movements—but if gene flow is frequent, such markers are unlikely to be found. In the meantime, detailed seasonal data for a variety of localities are very desirable.

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